

Parthenogenesis explained

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Abstract

The article considers the mechanism of parthenogenesis found in stick insects and the possible reasons it has developed. Reference is also made to other occurrences of parthenogenesis.

Key words

Phasmida, Parthenogenesis, Meiosis.

Introduction

How does parthenogenesis actually work? How widespread is it? What has actually been discovered about phasmid parthenogenesis? Does parthenogenesis affect the genetic variation of a species?

Parthenogenesis has fascinated me since I was a schoolboy. Many pupils who encounter parthenogenesis will probably do so through either the Indian stick insect, *Carausius morosus* (Sinéty), or the pink winged stick insect, *Sipyloidea sipyilus* (Westwood). Parthenogenesis is not restricted solely to phasmids. Aphids, such as greenfly, reproduce by parthenogenesis throughout the summer but in the autumn they reproduce sexually. In locusts and grasshoppers almost all the unfertilised eggs start developing, although few will develop into the adult. However it is possible to develop a parthenogenetic strain of locust (Wigglesworth, 1966) through artificial selection. Cockroaches and many species of Lepidoptera can occasionally develop from unfertilised eggs (Wigglesworth, 1966), even the familiar *Drosophila* can show parthenogenesis, *Drosophila mercatorum* having been maintained in culture for twenty years without males (Carson *et. al.*, 1982). There is even the phenomenon of parthenogenetic turkeys (Harada & Buss, 1981) although this is a bit of a dead end as all turkeys produced are male! For those who might want to look into the matter further, the explanation lies in the sex chromosomes.

Normal Sexual Reproduction (Meiosis)

In order to understand parthenogenesis it is necessary to first understand the normal process of sexual reproduction (see figure 1). Normal sexual reproduction uses reduction division (meiosis) to produce sex cells (gametes) with half the normal number of chromosomes. When the gametes fuse, at fertilisation, the normal chromosome number is restored. Without reduction division the chromosome number would double each time reproduction took place and the nucleus would grow until it filled the cell!

The first stage of meiotic cell division results in all the chromosomes replicating to give double the original number. However the new copy stays attached to the original and behaves as a single chromosome. The chromosomes move to form pairs (with the copy still attached), this stage is called pachytene. The pairs then move to the centre of the cell and then move to opposite poles, half to one side and half to the other, in anticipation of the cell dividing in two.

After this first division, the chromosomes line up in the centre of the cell and the chromosome copies, called chromatids, are now separated in a second division. The end result of this process, in which the cell replicates to give twice the number of chromosomes and then divides twice, is that the original cell gives rise to four gametes each with a chromosome number half that of the original ($\times 2 \div 4 = 0.5$).

The difficulty for a parthenogenetic species of stick insect is to restore the normal chromosome number without fertilisation. The Indian and pink winged stick insects have 66 and 80 chromosomes respectively (Pijnacker, 1978).

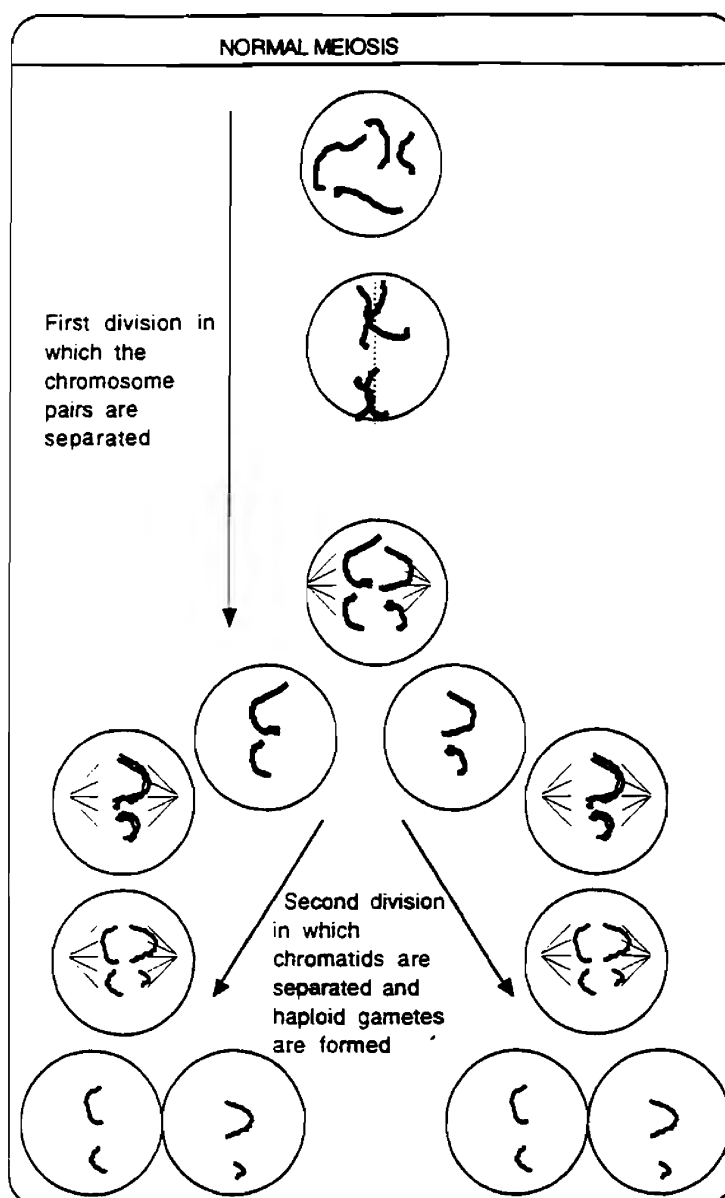


Figure 1. Chromosome separation during normal meiosis.

The Mechanism of Parthenogenesis

The cultures of both the Indian and the pink winged stick insects reproduce by obligate parthenogenesis (i.e. they are forced to use parthenogenesis), although this may not be the case in the wild (see the section on the origin of *Carausius morosus*). They both use the same mechanism to accomplish reproduction without males. There is an extra replication of chromosomes following pachytene so that meiosis starts with four times the original chromosome number. As a result there are four cells with the original chromosome number after meiosis ($x 2 \times 2 \div 4 = 1$). Each egg cell now has the correct number of chromosomes to divide and develops into a new stick insect (Pijnacker, 1964).

Earlier on in my studies I wondered how many eggs the meiotic divisions give rise to. Are there four viable eggs produced by the Indian stick insect? It would appear, that each cell which starts to undergo meiosis gives rise to a single egg. From Wolf's (1993: 103) comment "In a few groups, such as insects and crustaceans, no distinct polar bodies are formed. Instead, polar chromosomes are enclosed by nuclear envelopes, forming polar nuclei

that remain nonfunctional in the peripheral egg cytoplasm.", it would seem that all the meiotic events which take place, do so without the formation of separate and distinct polar bodies; this assumes that stick insects follow the same pattern as the other insects.

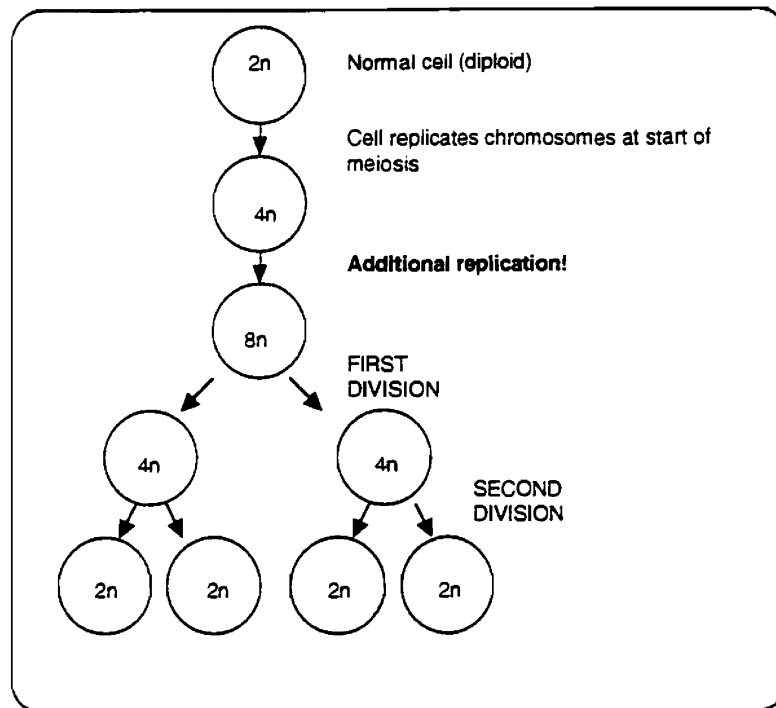


Figure 2. The parthenogenesis of *Carausius morosus*.

The eggs produced by the Indian stick insect and the pink winged are not haploid but diploid at the end of meiosis (Pijnacker, 1964 & 1978). This means that the rare males which are produced, when they mate, are trying to fertilise diploid eggs. Although mating has been observed it has no effect, indeed there is no evidence at present that sperm are transferred (Pijnacker, 1964). (see figure 2).

In *Bacillus whitei*, Nascetti & Bullini, the meiotic divisions occur as normal but two non-sister nuclei fuse to give a diploid egg (see figure 3). This is unsuccessful in 25% of the eggs however, which means a maximum hatching of 75% for the species (Mereschalchi *et al.*, 1991).

The Advantage of a Modified Meiosis

Why does the process have to be so complicated? To answer that question we must be aware of two things.

The first thing to realise is that meiosis produces totipotent cells, that is cells which can divide to give a whole animal (ordinary cells produced by mitosis are unable to do this). Once the stick insect has grown to an adult, cells become locked into developmental pathways to become legs, cuticle, eyes etc. Through meiosis the cell has the potential to become all these things. Research on frogs has shown that the cytoplasm of the fertilised egg cell plays a key role in triggering the fertilised egg to divide and produce the whole frog. If the nucleus from a fertilised egg is removed and a gut cell nucleus substituted then the embryo develops normally. This shows that the cell cytoplasm, ignoring the nucleus, is primed ready to divide (Wolfe, 1993). Even unfertilised frog eggs can be triggered to start dividing by pricking the cell with a pin dipped in human blood. Somehow the mechanical and chemical stimulation

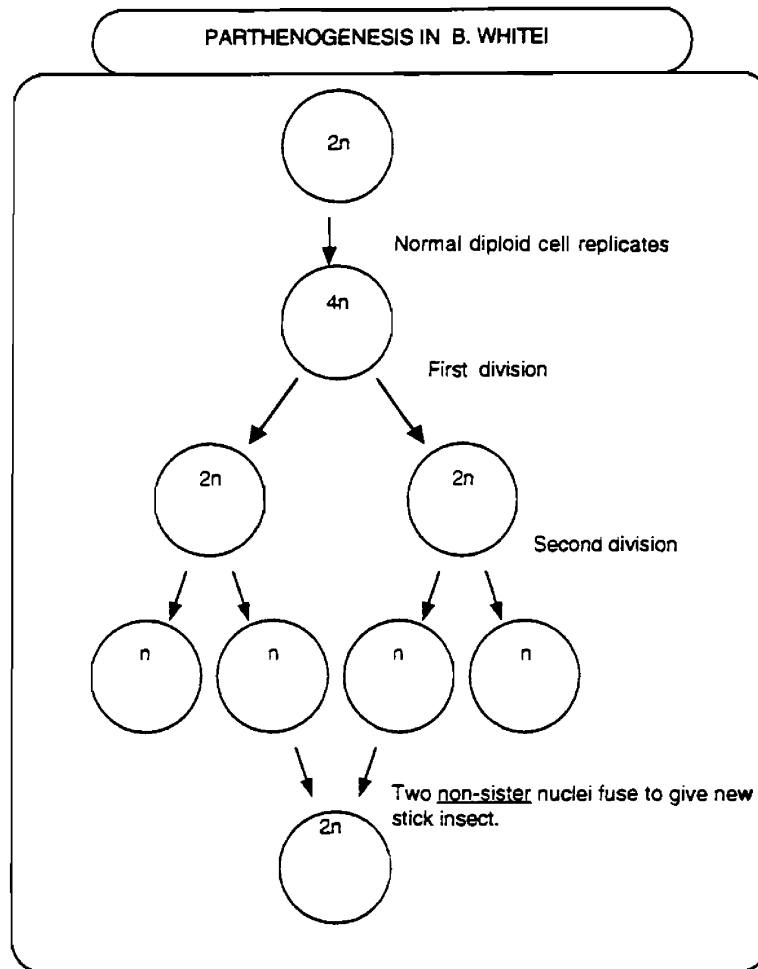


Figure 3. Parthenogenesis in *Bacillus whitei*.

starts cell division (Keeton, 1980). Applying this to stick insects, meiosis prepares the cell to divide and give a whole new organism; a major part of this seems to be outside the nucleus, in the cytoplasm. There is a brief discussion of the effect of the cytoplasm in embryogenesis in Siegfried Scherer's book *Typen des Lebens* (1993); he explains its significance in allowing a limited development of hybrid embryos.

The second thing achieved by meiosis is the resetting of the "biological clock". In cells there is a mechanism on the chromosomes which permits only a given number of cell divisions. As the cell divides, small sections from the end of the chromosome are missed out. Gradually the chromosome becomes shorter and shorter. It is this which causes cells to age and lose their ability to divide. These ends, called telomeres, are restored in meiosis by an enzyme called telomerase. This effectively resets the "clock", allowing all the cell divisions necessary for the life of the organism (Crompton, 1995). An analogy in computer software is the "counter", this protects copyright by permitting only a given number of copies.

So we can appreciate that parthenogenesis needs the normal aspects of meiosis and how they prepare the cell: the telomeres are added to reset the biological clock and the cell cytoplasm is made ready to develop into a new stick insect.

The Origin of *Carausius morosus*

A suggestion of Pijnacker (1964) is that the Indian stick insect may have arisen through

chromosome duplication. This would give rise to an autotetraploid individual: tetraploid because it would have four of each chromosome, and auto because it is an event occurring within itself which has caused the duplication.

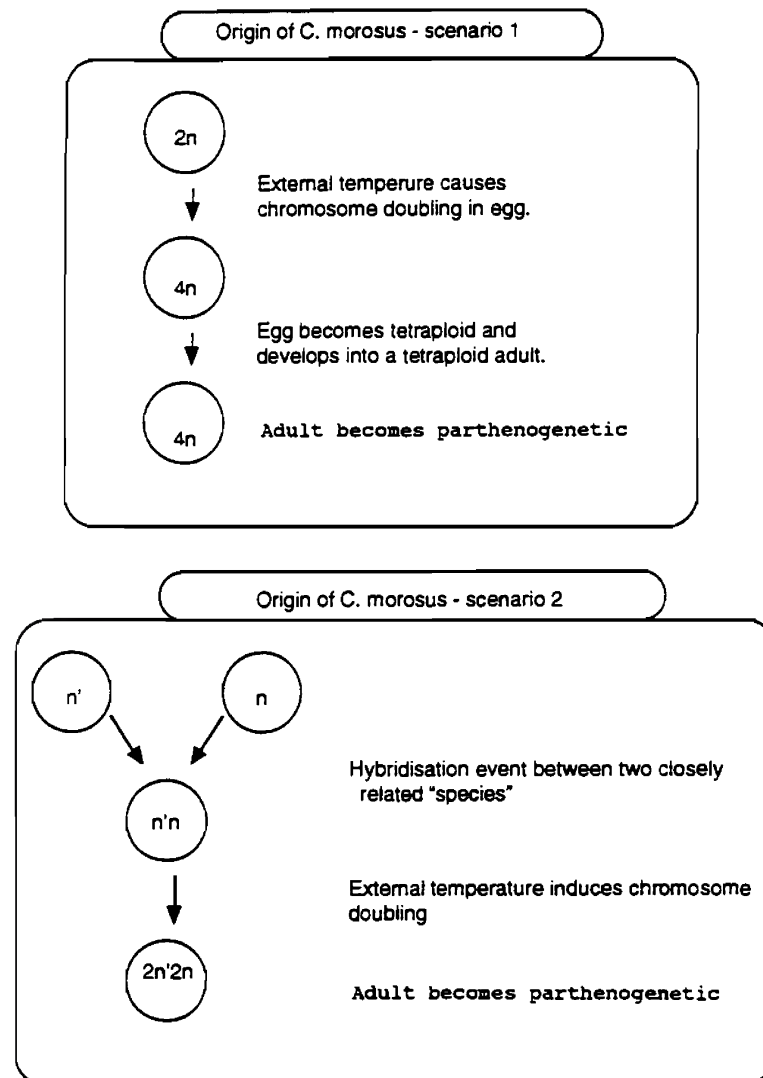


Figure 4. Origin of *Carausius morosus*.

Such an individual may have been induced by cold temperatures (similar to the effects of hyperbaric pressure or heat shock treatment). That could cause chromosome doubling in the embryo. Pijnacker (1964) notes that the area where *Carausius morosus* was collected commonly has temperatures which might have a similar effect. Once fully grown it would produce eggs with twice the normal number of chromosomes (see figure 4, scenario 1).

A second possibility is that two stick insects hybridise. This could produce problems for sexual reproduction if the chromosomes could not pair properly. If an egg were to experience chromosome doubling each would have a matching chromosome to pair with. Then it could undergo meiosis and develop the extra replication which allows parthenogenesis, (see figure 4, scenario 2). This has become more likely with the discovery that *Bacillus whitei* is a hybrid of *Bacillus rossius* (Rossi) and *Bacillus grandii* Nascetti &

Bullini and that *Bacillus lynceorum* Bullini, Nascetti & Bianchi Bullini is a hybrid of *Bacillus rossius*, *Bacillus grandii* and *Bacillus atticus* Brunner (Mareschali *et. al*, 1991).

How does Parthenogenesis Affect the Health of the Species?

Does the parthenogenesis of the stick insects lead to a homozygous individual? It is generally acknowledged that the homozygous condition shows up harmful genetic mutations which could be masked in the heterozygous condition. This is why corn, which quickly becomes homozygous through self fertilisation, shows a marked decline in vigour after several generations. Is there a similar decline in vigour of stick insects which reproduce by parthenogenesis?

In the pink winged stick insect where the fusion of non-sister polar bodies occurs we can predict the maintenance of the parental genotype with no increase in homozygosity. In the Indian stick insect (and others that show an additional replication before reduction) the heterozygosity of the mother is preserved in the daughter. So in these cases vigour should not be affected.

Why Parthenogenesis?

Are there any advantages in parthenogenesis for the stick insect? Clark (1973) lists eleven factors associated with parthenogenesis. The most relevant are listed below (using Clark's numbering).

1. Environmental instability and the exploitation of temporary resources.
4. Reduced motility of females.
5. Infrequency of males either through genetic drift or low fitness.
6. Polyploidy, aneuploidy, male haploidy
8. Discontinuous habitats.
9. Colonising habitats.

Parthenogenetic stick insect populations are able to grow quickly because all are females. This should be compared with a sexual species where 50% are non-egg laying males. Quick population growth is an obvious advantage in transient habitats.

As regards Clarke's 5th factor, it is interesting to note that males are produced in *Carausius morosus*, however they are not virile with much less than 1% spermatozoa appearing normal (Pijnacker, 1964). For those of you who think you might have a male *C. morosus* look for the following:

- i) The male is slender and shorter than the female due to five instead of six moults.
- ii) The male chitinous skeleton appears smooth and glossy instead of matt and granular.
- iii) The male has a red mesosternum, two red stripes laterally on the mesothorax and two red spots laterally on the metanotum.
- iv) The male external genitalia consists of a single asymmetrical penis covered by an operculum which is the sternum of the ninth segment.

For the triploid *Bacillus lynceorum* with three sets of chromosomes, it could not create the chromosome pairs needed for meiosis unless it first underwent an extra replication. When it does so it then has six sets of chromosomes it then can undergo the reduction divisions of meiosis restoring it's triploid chromosome number. A similar problem is encountered by the banana: it too is triploid and because of that cannot reproduce sexually by meiosis. It is a common and widespread plant however, widely grown by the Polynesians in the Pacific. Propagation is by means of cuttings which they took with them as they colonised new islands. This is also the reason why you do not find seeds in bananas, their triploid nature means they

cannot produce seeds.

The Occurrence of Parthenogenesis

Parthenogenesis is probably more widespread than we know. In some species parthenogenesis may be so rare that it passes unnoticed. In *Bombyx mori* only one moth was obtained from 10,000 unfertilised eggs (Engelmann, 1970). The potential for parthenogenesis has been realised for some species in the laboratory. An original bi-sexual stock of *Drosophila* has actually served as the exclusive source of four separate parthenogenetic strains isolated in 1961 and 1962 (Carson, 1982). It is not uncommon then for there to be a naturally present, low grade facultative parthenogenesis. In the wild this could be realised in two ways, one is isolation and the other is competition.

Geographical isolation could arise by individuals founding new populations in new habitats. If a few individuals with a reasonable occurrence of parthenogenesis were to colonise a new habitat females might experience difficulty in finding mates. Laying unfertilised eggs, only the parthenogenetic ones would produce adults which would obviously be females. With extremely strong selection for parthenogenesis it would not take long for a parthenogenetic race to develop. Parthenogenesis has the potential to out-compete bi-sexual races because with all the population being female they should be able to reproduce twice as quickly. Once established they would be able to out compete any sexually reproducing relatives that arrived subsequently. In genetics this would be described as a "bottleneck" or possibly "the founder effect", with a handful of specimens isolated from the rest of the population reproducing to give a new population.

In applying this to *C. morosus* we must remember that although it has been studied intensively, it is laboratory cultures which have been studied. We know that the cultures are parthenogenetic but we cannot speak so assuredly of the wild population. According to Pijnacker (1964) the original Indian stick insects seem to have been introduced to Europe about 1911 or 1912, but Ragge (1973: 229) has pointed out that there have been several importations and it has been in culture since the 1890s. It would appear to be from this original stock that all Indian stick insects have been bred.

One of the stories I heard when chasing up a report of a male Indian stick insect was that the males in the original population had died out leaving only females. If true this would have created strong selective pressures on the remaining females, in favour of parthenogenesis. If there were any noticeable differences in that original sample that may have affected their subsequent growth as a population. One of those differences in the original collection, which may have helped the spread of parthenogenesis in a "bottle-necked" population of *Carausius morosus*, may have been stick insects which could already reproduce poorly by parthenogenesis or the poor fertility of males: Clark's 5th factor.

A different pressure towards parthenogenesis has come from hybridisation and polyploidy. Hybridisation can lead to all sorts of problems during homologous pairing in meiosis, i.e. *Bacillus lynceorum* and the previously mentioned banana. In plants there is always the potential for asexual propagation by runners which can be very successful; indeed *The Guinness Book of Records* (Matthews, 1993) has a Quaking Aspen listed, which reproduced asexually by roots, to occupy 106 acres and weigh an estimated 6,000 tonnes. This is not an option for animals such as stick insects. Their equivalent is to reproduce by parthenogenesis. So, for the stick insects with mismatched sets of chromosomes (Clark's 6th factor), parthenogenesis is a their only option.

Both geographical isolation and the problems of polyploidy seem to come together in the Alps. Engelmann reports the work of Suomalainen on geographical races of the Curculionidae (Insecta: Coleoptera) in Scandinavia and the Alps. This shows a correlation

between polyploid parthenogenetic species and new habitats exposed at the end of the last Ice Age (Engelmann, 1970). It would appear that they were either better able to sustain the more adverse climatic conditions or that they followed the retreating ice and entered new habitats: Clark's 9th factor.

Table 1. Summary of information on the species mentioned.

PSG culture	Species	Chromosomes	Reproduction	
1	<i>C. morosus</i>	2n = 66	Parthenogenetic#	Hybrid with chromosome doubling.
4	<i>S. sipylus</i>	2n = 80	Parthenogenetic#	
108	<i>B. whitei</i>	2n = 35	Parthenogenetic*	Hybrid of No. 172 & 3.
107	<i>B. lynceorum</i>	3n = 52	Parthenogenetic#	Triploid hybrid of No. 172, 3 & 156.
172	<i>B. grandii</i>	?	Sexual	
3	<i>B. rossius</i>	?	Sexual	
156	<i>B. atticus</i>	?	Sexual	

Key: # = additional replication at start of meiosis.

* = fusion of non sister nuclei from second meiotic division.

Summary

That the parthenogenetic stick insects have their origins in the sexual species is clear. They can maintain their existing genetic variation (heterozygosity) but cannot add to it. Moreover such genetic variation as they possess is not available to give new combinations because each daughter has the same genotype and phenotype as her mother. On the positive side they can reproduce more quickly as an all-female race both to exploit temporary resources and colonise new habitats. Table 1 gives a summary of the information which I have been able to find about the species which I have mentioned.

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